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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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TORREY BOTANICAL CLUB

JULY, 1923

Studies on plant cancers—IV. The effects of inoculating various quantities of different dilutions of Bacterium tumefaciens into the tobacco plant*

MICHAEL LEVINE

The early studies of dosage center about the question of the transmission of tuberculosis and date back to the period shortly before the discovery of tubercle bacilli. Tappeiner (1878–1880) was among the first to test the effect of crudely measured quantities, such as a teaspoonful and a tablespoonful, of sputum of a tubercular patient sprayed into the respiratory tract of a dog. In 1890, Gebhardt, under favorable and aseptic conditions, studied the effect of inhalations of tubercle bacilli and also intraperitoneal and subcutaneous injections of the same organism into the guinea pig. He used the expressed milk of the udder of tubercular cows, the sputum of phthisis patients, and pure cultures of the bacillus grown on beef-peptone-glycerine. With the pure cultures he used 5 cmm. to 2 cc. sterile water. This suspension was diluted 1 : 400 and used as a mother liquor. Intraperitoneal injection of a dilution of the mother liquor in a proportion of 1 : 500 gave tuberculosis. Very dilute suspensions induced tuberculosis by inhalation and subcutaneous injections. Preyss (1891) made a more determined effort to establish the quantity of tubercle bacilli necessary to cause tuberculosis. He found that a droplet 1/1000 mg. of sputum which contains forty tubercle bacilli was sufficient to induce tuberculosis in the guinea pig. He made no actual count of this number but estimated it on the basis of 1 mg. moist culture of tubercle bacilli, which he claimed contained thirty-five million organisms.

* From the Cancer Division, Montefiore Hospital, Dr. Isaac Levin, Chief.

[The BULLETIN for June (50: 197–230. *pl. 9–12*) was issued July 6, 1923.]

Huytra (1905), in studying the effect of von Behring's inoculating fluid in immunizing cattle against Bovine tuberculosis, used 0.004–0.025 gm. of Bovine tuberculosis to produce this disease. Findel (1907) studied the difference between inhalation and feeding as methods for inducing tuberculosis. He used dogs, calves and guinea pigs. Like Preyss he calculated that by certain spray methods he was able to induce tuberculosis in the guinea pig with twenty tubercle bacilli and suggests that only one bacillus is sufficient to infect the guinea pig. Theobald Smith (1908) in studying Bovine tuberculosis, immunized cattle by injections of 5–300 mg. of dry weight of tubercle bacilli of the human of different ages. The number of individuals in these masses of bacteria was not estimated.

Barber (1907), studying the transmission of the characters, size, and form in *Saccharomyces anomalus*, *Bacillus coli communis*, *B. typhosus* and *B. megatherium*, devised an isolation pipette whereby he was able to make a culture from a single cell. By this method he was also able to inoculate a mouse with three to six bacilli of anthrax obtained from the blood of another mouse with this disease. Webb, Williams and Barber (1909) studied the method of immunizing an animal against a specific disease by inoculating the animal with small doses of bacteria, beginning with a single cell and then increasing the number. In this work the isolation pipette was used so that the cells were seen, counted and then inoculated. This was done for typhoid, anthrax and tuberculosis.

Wyssoskowicz (see Adami, 1908, p. 185) claimed that the minimal dose required to induce tuberculosis in guinea pigs was eight tubercle bacilli; while twenty-four to thirty were required for the rabbit.

A voluminous literature dealing with the effects of measured doses of inoculum in animals has developed in the last two decades, but these studies were made in connection with work in immunity, distribution of parasites, etc., and with no special reference to the question under consideration here.

While I have been unable to find in the literature any reference to dosage studies with bacterial parasites of plants, Cobb (1904–1905) suggested that the degree of infection of a crop of wheat with smut could be determined by counting the number of smut spores that could be removed from the seed samples.

He washed seed samples and calculated the spore content of the washings by counting the spores of a given quantity of washings against red blood cells. While Cobb was the first to count spores of parasitic diseases of plants Bolley (1902) first suggested the use of the centrifuge in removing the spores from seeds for microscopic determination. Heald (1921) took up the work of Bolley and Cobb and devised new methods for calculating the number of spores of smut per wheat grain. He planted seeds with a known spore number and then estimated the degree of smutting in the crop. Heald also infected wheat with known quantities of smut spores and determined the degree of infection in the crop. For example, he determined that 0.5—3 gm. of air dry spores per hundred wheat grains gave maximum smutting. Heald contends that there seems to be a gradual increase in the percentage of smut in a crop with an increase in the number of spores carried by each grain. He does not believe that infection of wheat with bunt can be accomplished by a single spore.

My earlier studies on crown gall in sugar beets (Levine, 1921) dealing with the effect of soil conditions on the health of the host and the size of the crown gall produced by inoculation have led me naturally to the problem of what the quantity of bacteria used in the inoculum has to do with the size of the crown gall. This study was started simultaneously with the study of the effect of soil conditions on the size of the crown gall in 1920 and was continued in the following year, 1921. While the results are not complete, the data obtained so far, seem to be of sufficient interest to warrant this report.

METHODS

During the month of May 350 tobacco seedlings sent from Virginia, varying in height from 6 to 10 inches, were set out in uniformly treated soil under similar light and moisture conditions. Toward the latter part of July and early August the plants were inoculated with *Bacterium tumefaciens*. Eight different emulsions of four different ages were used as inocula. These cultures were grown under uniform laboratory conditions and on a medium which consisted of 50 gm. beans, 1 l. water, 15–20 gm. agar agar. Enough of the medium was poured into 150 cc. Erlenmeyer flasks to cover the bottom to a depth of 1 cm. The

medium was then inoculated by pricking the surface of the agar in five to eight different places with a needle containing a subculture of *Bacterium tumefaciens*. After the bacteria had multiplied for from two to forty days the surface of the agar was gently scraped to avoid as far as possible the removal of portions of the surface of the agar. I employed two methods for inoculating my plants. The first, a modified form of the commonly used pricking method, and the second, the trocar method. In the first method the cylinder of a medium-sized hypodermic needle was filled with paraffin so as to convert the point into a spoon-like container. This was dipped (into an emulsion of *B. tumefaciens*), so that the spoon end of the needle alone contained the bacteria. This was then gently stuck into the plant at a desired point, five to ten times, until all the emulsion was removed into the plant. For larger measured quantities of bacteria the second method was used. A plug of tissue 3–5 mm. long and 0.5 mm. in diameter was removed from the part of the plant where the inoculation was to be made by a trocar. The suspension of the crown gall organism was then introduced through a graduated hypodermic syringe. Numerous controls were made by removing a plug of tissue and filling the cavity with sterile water.

All mother emulsions consisted of 4 cc. of such culture scrapings of *B. tumefaciens*, to which was added 2 cc. of sterile water to facilitate the removal of the bacteria from the surface of the agar. The following dilutions of these cultures were made and will be referred to in the text by number.

Emulsion Ia is from a culture of *Bacterium tumefaciens* 21 days old. Subdilutions of this culture were made by the addition of sterile water in the following proportions: *Ib*, 1 : 1; *Ic*, 1 : 10; *Id*, 1 : 20.

Emulsion IIa is from another set of cultures of *Bacterium tumefaciens* 21 days old. *IIb* consisted of a part of the emulsion, *IIa*, diluted with an equal part of sterile water. In *IIc*, the dilution was made in the ratio 1 : 3.

Emulsion IIIa is from a third group of cultures grown at another later period used at the age of 21 days. In *IIIb*, the dilution is made in the proportion 1 : 5; in *IIIc*, 1 : 10; in *IIId*, 1 : 15; in *IIIe*, 1 : 25.

Emulsion IV represents still another set of cultures 21 days old. This was used undiluted.

Emulsion V is from cultures of *Bacterium tumefaciens* 40 days old.

Emulsion VIa is an emulsion from young cultures 2 days old. *VIb* was diluted 1 : 15; *VIc*, 1 : 10; *VId*, 1 : 20; *VIe*, 1 : 40.

Emulsion VII is an undiluted mother emulsion seven days old.

In the latter part of October harvesting began. The plantation had been plotted for identification of the test plants early in the season. Each test plant was now carefully removed from the soil. The diameters of the more globular crown galls were measured in several axes, averaged and recorded. The averages of these measurements for a number of plants are shown in the TABLE below. Leafy crown galls and axillary leafy crown galls were also measured although obvious difficulties were met in doing this.

OBSERVATIONS

While to actually count the number of *Bacterium tumefaciens* inoculated in a given case was impossible yet dilutions of emulsions of the organisms sufficiently different were used to show contrasted effects, if any be produced in this way. In 1920, two hundred midveins of sixty well grown tobacco plants were inoculated with dilutions of *Bacterium tumefaciens* from culture fourteen days old. The dilutions were made in the following proportions: A, 1 : 100; B, 1 : 50; C, 1 : 25; D, 1 : 15; E, 1 : 2; and F, 1 : 1. The crown galls which resulted were all approximately the same size. Each intumescence measured approximately 0.2–0.3 cm. in diameter. These results were followed up by further studies in 1921. The TABLE shows the results. In general, they confirm the preliminary studies. In these later studies the stems were also inoculated at the node and internode as mentioned below.

Emulsion Ia was made by collecting 4 cc. of scrapings from a flask culture of *Bacterium tumefaciens* and diluting as noted above. Dilution Ib consisted of 1 cc. of the emulsion mixed with an equal part of sterile water. Dilution Ic was mixed in proportion of 1 : 10 parts of water; Id, 1 : 20; and Ie, 1 : 30. Forty-seven plants of uniform size and age and growing in the same plot were inoculated with one drop of Emulsion Ia, b, c, d, and e, of *Bacterium tumefaciens* in trocar incisions made in the axils of the upper leaves. The size of the crown galls was measured at the end of the season and found to be more or less uniform, varying within the range of the variation in size found in the individual plants. Dilution Ia inoculated into twenty-two plants by the trocar method gave an average size crown gall 1.8 cm. in diameter. While Id and Ic, dilutions ten to twenty times weaker, gave an average size crown gall slightly

larger. Id gave approximately the same results as Ib (see TABLE).

When the axil of an upper leaf of a decapitated plant was similarly treated, the average size of the crown gall for the four

AVERAGE SIZE ** OF CROWN GALL ON TOBACCO RESULTING FROM INOCULATIONS WITH VARIOUS EMULSIONS OF BACTERIUM TUMEFACIENS

Emulsions and dilutions	Character and quantity	Age of culture	No. of plants	Mid-vein leaf	No. of plants	Stem	No. of plants	Leaf axil	No. of plants	Leaf axil of decapitated plants
No. I										
a	1 drop trocar method	21 days			5	1.5	22	1.8	10	2.3
b							10	2.2	9	1.9
c							7	2.3	8	2.3
d							8	1.9	10	2.7
d[1]	0.8 cc.*						20	1.9		
No. II										
a	1 drop 5–10 needle pricks	21 days					11		1.2	
b							9		1.3	
c							12		1.5	
a[1]	1 drop trocar method						12		1.9	
c[1]							16		2.3	
No. III										
a	1 drop trocar method	21 days	5	0.3	5	1.6				
b			5	0.3	5	1.06				
c			5	0.3	5	0.6				
d					5	2.3				
e					5	1.8				
No. IV	1 drop 5–10 needle pricks	21 days	6	0.9						
No. V	1 drop 5–10 needle pricks	40 days	6	0.5						
No. VI										
a	1 drop trocar method	2 days			5	1.6			4	2.1
b					5	2.2			13	1.5
c					5	2.			14	3.2
d					5	2.6			4	1.6
e					5	3.1			4	3.5
a[1]	0.25 cc.*						16	2.7		
No. VII	trocar method									
a	0.28 cc.*	7 days	15	0.7						
b	0.5 cc.*		11	1.2						

* Average quantity.
** Size given in cm

dilutions used was more or less uniform. The average size of the crown gall produced by dilution Ic was 2.3 cm. while Id (in which the suspension was 1 : 20) gave a crown gall which averaged 2.7 cm. in diameter. The same general results were obtained with dilutions of Emulsion VI (see TABLE) when inocu-

lated into the stem and leaf axils of decapitated plants by the trocar method. Here in the thirty-nine plants studied, the largest crown galls were produced with the weakest suspension, 6e. Yet the variations were slight and if a sufficient number of cases had been available, it is believed the average size of the crown galls would probably have been more nearly alike. The fact still remains, however, that the smallest crown galls were produced with suspensions bearing the largest number of bacteria.

The inoculation of the upper axillary buds of decapitated stems showed that 6c and 6e gave results more than double those of 6b and 6d, respectively. The dilution in each case was half the strength of those that gave the smaller growths.

Inoculating the midveins of leaves with the dilutions of Emulsion III listed above, gave more consistent and uniform results. In fifteen plants so studied the average diameter of the crown galls was 0.3 cm. The inoculations of the stem gave quite a range in size of the galls produced, but here again as shown for the other two series the number of bacteria did not obviously influence the size of the growths. The sizes of the crown galls seemed to be correlated with the individual variations in the sizes of the plants, but here again emulsion dilution 3d (1 : 15) gave crown galls almost twice as large as those obtained with 3a, which is the mother emulsion.

Inoculating these plants by pricking them with a needle capable of holding a uniform quantity of bacteria gave approximately equal results, which shows that the number of bacteria or strength of the emulsion within the range tested is not directly concerned with the size of the crown gall. Emulsion II was used in inoculating thirty-two plants by dipping the point or spoon-like end of a filled hypodermic needle into emulsion IIa, b ,and c of *Bacterium tumefaciens*, and then pricking the plant with the point of the needle. The inoculated plants showed at the end of the growing season that the more concentrated suspension of *Bacterium tumefaciens* did not produce the largest gall. As it happened, it produced the smallest.

Comparing the trocar and the needle method of inoculation as used, cultures IIa and IIc—IIa′ and IIc′ (the latter two cultures indicate similar dilutions but used with the trocar) show somewhat larger galls for the trocar method. The differences, however, do not appear to be significant. The weak dilution

produced growths which averaged 0.4 cm. larger than the dilution which was three times the strength of the first. It seems from these studies that for uniformly aged cultures and equally well developed plants a drop of the weakest suspension used when inoculated into the stem or midvein of a tobacco plant incites a crown gall development as large as a suspension forty times more concentrated.*

COMPARISON OF THE REACTIONS OF DIFFERENT PARTS OF THE PLANT TO EQUAL QUANTITIES OF THE SAME DILUTION

Striking differences were found among the crown galls resulting from inoculations with equal quantities of the same or similar dilutions of *Bacterium tumefaciens* when placed in different parts of the plant. This appeared to be true regardless of the quantities of bacteria or strength of the emulsion used. The crown galls on the midveins of leaves were invariably smaller than those on the stem and these in turn were smaller than those that developed at the axil of a leaf. The inoculated axillary bud of a decapitated plant produced generally the largest crown gall.

For example, the sizes of crown galls obtained with Emulsion III a, b, and c on the leaf vein and the stem show that equal quantities of bacteria produce in the stem a neoplastic growth considerably larger than on the midvein of the leaf. Comparing the tumor growths in the leaf axils with those of the stem internode produced by equal quantities of the same emulsion (see TABLE, Emulsion I) shows a slightly larger growth in the axil. The inoculation of Emulsion Ia into five stem internodes pro-

* Since the above data went to the press I had the opportunity to study further, weaker suspensions of *Bacterium tumefaciens* and the effect of inoculations of one drop and 0.5 cc. of these solutions at the leaf axils of young geranium plants. I used 3 cc. of the scrapings of a twelve day culture of *Bacterium tumefaciens* and suspended 1 cc. in 500, 750, and 1000 cc. of sterilized tap water.

The plants which received 1 drop or 0.5 cc. of the 1:500 solution produced small crown galls which averaged 4 mm. in diameter forty-five days after the inoculation. The plants which received 1:750 and 1:1000 solution, in only a very small percentage of inoculations, were crown galls produced. Those that developed were approximately 3–4 mm. in diameter, and in general, were equal in size to those produced by inoculations with undiluted *Bacterium tumefaciens*.

duced crown galls which averaged 1.5 cm. while inoculation in the axils with similar quantities of the same emulsion gave an average growth 1.8 cm. for twenty-two plants. The result here really suggests a summation of the stimulus from the bacterial organism and the natural budding tendencies of the tissues in the leaf axil if indeed, there is not an actual bud with more or less active growth tendencies in the axil of every leaf.

When the size of the crown gall in the axil of a leaf of a normal plant is compared with that in the axil of a leaf of a decapitated plant it is found that the axillary crown gall is larger (see TABLE Emulsion I). A comparison of the size of the crown galls on stem internodes with those in the axillary buds of decapitated stems produced in each case by equal quantities of the same dilution shows much larger crown galls for the decapitated plants; (study TABLE, Emulsion IV). It appears that the size of the galls produced by equal quantities of similar or identical suspensions of *Bacterium tumefaciens* inoculated depends upon the location of the inoculation. The midvein of a leaf shows the smallest crown gall reaction; while the axil of a leaf of a decapitated stem shows the largest growth. This was of course already implied in the general comparison of galls from different parts of plants.

RELATIVE VIRULENCE

It is a well recognized fact in general old cultures of pathogenic bacteria are less virulent than young cultures. The cultures used in these experiments were subcultures of *Bacterium tumefaciens* (hop strain) sent to this laboratory by E. F. Smith in 1917. These had been kept in culture and used in my former experiments. When the present experiments were started cultures varying from two to one hundred and ninety days old were available. The latter were too dry to warrant any attempt at use. Cultures two days old were made up into various dilutions (Emulsion VI) of which 6a is the undiluted culture drived by scraping the media upon which the organisms were growing. The crown galls which resulted from inoculating the stem internode with this culture showed an average of 1.6 cm. in diameter. Emulsion 3a which is an undiluted culture of *Bacterium tumefaciens* twenty-one days old grown under the same conditions as Emulsion VI also gave crown galls of an average diameter of 1.6

cm. But when these results are contrasted with crown galls resulting from Emulsion 1a, another culture twenty-one days old, the growths resulting from the younger cultures are seen to be slightly larger. Comparing the size of the crown galls in axillary buds the young cultures and the old produced results almost identical; (compare Emulsions I and VI). Cultures twenty-one and forty days old were contrasted by inoculating Emulsions 4 and 5 into midveins of leaves. The larger growths appeared on the leaves which were inoculated with the younger bacteria. Yet the inoculation of Emulsion V in the midvein of the tobacco leaf produced a larger growth than did Emulsion III, another culture twenty-one days old. It appears that so long as the *Bacterium tumefaciens* is viable the age of the culture has little effect on the size on the gall produced. A culture two days old is no more effective in producing crown galls in tobacco than are cultures three to five weeks old.

THE EFFECTS OF VARIOUS QUANTITIES OF SIMILAR DILUTIONS

The size of galls produced when different quantities of similar dilutions of *Bacterium tumefaciens* were inoculated in the tobacco was compared. Comparing results with the prick and the trocar methods it seems that inoculation through a trocar wound produces a slightly larger growth than is produced by pricking the plant five to ten times with a needle carrying an emulsion of the same dilution; (compare 2a and 2a′). The difference may be explained, however, not on the basis of the quantities of the bacteria introduced, but on the degree of injury to the cells caused by the trocar method as compared with the pricking method.

When two different quantities of *Bacterium tumefaciens* were inoculated by the same method the difference in results was negligible. One drop of emulsion Id and 0.8 cc. of the same emulsion called Id′ (for convenience of record) were inoculated into axillary buds of the tobacco. Similar results were obtained. The average size of the crown gall in each series of experiments was 1.9 cm. Sixteen plants were inoculated in the leaf axils with an average dosage of 0.25 cc. of emulsion 6a′ (an emulsion equal to 6a in strength). While these results were not compared with those obtained by using a drop of 6a in the leaf axil it was found that the average size of the growths with 0.25 cc. of

Bacterium tumefaciens in the leaf axil was 2.7 cm. which is slightly larger than the average for galls produced by inoculating the axil of a leaf of a decapitated plant with 6a and smaller than the average for galls resulting from a drop of 6e (forty times weaker) inoculated in the leaf axil, a region which gives the maximum reaction to the crown gall organism.

SUMMARY AND CONCLUSION

1. Tobacco plants of uniform age and size and growing under uniform conditions of soil and light were inoculated with *Bacterium tumefaciens* to determine the effect of various dilutions of a given culture on the size of the crown gall produced. In these experiments I have not counted the organisms in the inoculating medium, but have used measured quantities of inoculum varying from ordinary agar culture emulsion to dilutions 1 : 100.

2. No constant difference was noted in the size of the crown gall resulting from an inoculation with the undiluted bacterial emulsion and a suspension forty times weaker.

3. The difference in the quantity of the suspension inoculated showed that the quantity of *Bacterium tumefaciens* was not effective in increasing the size of the gall. The differences observed when trocar and needle are compared must be referred to the relative degree of injury and number of cells exposed.

4. Suspension from cultures of *Bacterium tumefaciens* two days old were found to be no more effective in producing crown gall in tobacco than were cultures twenty-one and forty days old.

5. It is concluded that the number of cells of *Bacterium tumefaciens* inoculated into the tobacco is not significant in determining the size of the crown gall. A smaller number of bacteria favorably lodged in tissue capable of response will produce a crown gall equal in size to that produced by a larger number.

6. The size of the crown gall is rather dependent upon the region of the host inoculated and the vitality of the host, than upon the number of bacteria starting the infection.

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Diagnoses of American Porias—II*

L. O. Overholts

(WITH PLATES 13 AND 14 AND THREE TEXT FIGURES)

PORIA CORTICOLA (Fr.) Cooke, Grevillea **14**: 113. 1886
Polyporus corticola Fr. Syst. Myc. **1**: 385. 1821.

Original Description: Effusus, firmus, glaber, albus, punctis confertis nudis. Duplex status lectus: a) *populneus*, seriato-elongatus, confluens, crassior, adhaerens, tuberculosus, pallescens, margine spurio tumido villoso, punctis rotundis aequalibus. b) *fagineus*, latissime effusus punctis integris. Ad cortices putridos. Populi. b. Fagi. Per annum (V.V.).

Redescription: Annual, soft and watery when fresh, broadly effused for many centimeters where best developed, separable when mature but young specimens closely adnate, typically with a thin pubescent, narrowly sterile margin, but this sometimes completely fertile and sometimes broadly sterile and membranous; subiculum very thin, inconspicuous, white, not more than 0.5 mm. thick; tubes unstratified, 2–5 mm. long, the mouths white when fresh, white or more commonly yellowish (cinnamon buff) on drying, often glistening, angular, very thin-walled, entire or becoming finely dentate-lacerate, averaging 2–4 per mm.; spores ellipsoid or oblong-ellipsoid, smooth, hyaline, commonly showing a tendency to cohere in groups of two to four, 4.5–5.5 × 3–3.5 μ; cystidia various, but usually present, either as fusoid projecting bodies, as smaller fusoid capitate-incrusted organs, or as entirely incrusted projecting organs, all 3–7 μ diameter; hyphae rather flexuous, simple or sparingly branched, with occasional cross walls but no clamps, diameter 2–4 μ in trama, 3–6 μ in subiculum.

On bark and wood of deciduous trees; recorded from *Acer*, *Fagus*, and *Populus*.

Specimens Examined: Swan River, Manitoba, Canada; Winnipeg, Manitoba, Canada (three collections); Harrisville, New York; Stone Valley, Pennsylvania; Chain Bridge, Maryland; West Elkton, Oberlin, and Oxford, Ohio; Creve Coeur Lake, Missouri (two collections); Custer, South Dakota; Missoula, Montana; Priest River, Idaho.

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* Contribution from the Department of Botany, The Pennsylvania State College, No. 42. For the first paper of this series, see Mycologia **14**: 1–11. *pl. 1 + f. 1–6.* 1922.

P. corticola is a soft white species (PLATE 13, FIGS. 1, 2) that appears to be fairly common from New York to the Rocky Mountains. Egeland (Norsk. res. Poresv. p. 143) reports it as occurring chiefly on aspen and birch in Norway. My records show *Acer* (including *A. Negundo*) to be its common host though found on both *Populus tremuloides* and *P. trichocarpa*. In the Ohio Valley it seems to frequent the beech. Sometimes it is strictly a bark-inhabiting fungus but just as frequently it grows on decorticated wood, particularly wood in advanced stages of decay—a fact that is responsible for the lack of information in many collections as to the exact substratum.

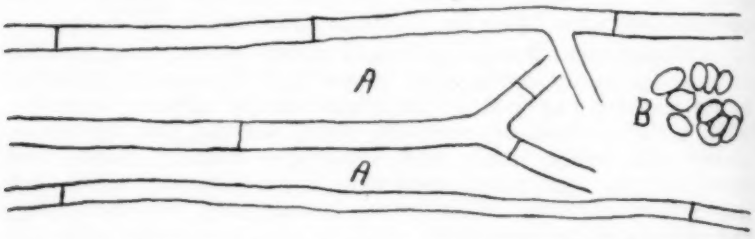


FIG. 1. PORIA CORTICOLA (Fr.) Cooke. A, Hyphae showing cross walls and absence of clamp connections; B, Spores, some characteristically agglutinated in groups.

As here interpreted the species is, in its microscopic characters, quite a variable one. Our American plant differs so markedly in the matter of cystidia that it might well be held to be at least a separate variety. In the European specimens I have examined and as reported by Egeland (Norsk. res. Poresv. p. 143), conspicuous cystidia are present in the hymenium. PLATE 13, FIGS. 3, 4, show these bodies as seen in plants from Sweden. Egeland also reports, and I have verified his statement in my study of Swedish specimens, that other bodies, which he terms paraphyses, with capitate-incrusted apices, are present with the cystidia, and in fact in some specimens I find this to be about the only cystidium-like organ present. In American collections the type of cystidium that approaches nearest to the well-developed form in European specimens is shown in PLATE 13, FIG. 5, made from a Pennsylvania collection taken in 1920, though they have been seen occasionally in another collection from Ohio. More frequently the capitate-incrusted type is present,

as seen in PLATE 13, FIG. 6; and this type grades over into a more heavily incrusted form, as represented in PLATE 13, FIG. 7, where they have the form and appearance of those found in *Fomes connatus*. Indeed, in the absence of spores, I had previously referred specimens of this type to a resupinate condition of that species.

The close microscopic agreement of all the plants with these variable structures and with other characters mentioned below, and the gradations and apparent relationships of these structures themselves seem to imply a relationship that can be readily embraced within the limits of a single species. About the only other American plant that shows cystidia comparable to those of the European *P. corticola* is *P. aurea* Peck, which seems to differ sufficiently in the shape and size of the spores, the presence of clamp connections, and other features, to warrant keeping it distinct.

Nearly all of the specimens I have referred to this species have another peculiar microscopic character in the tendency of the spores to cohere in groups of two to four (TEXT FIG. 1). The hyphae are also more or less distinctive in the presence of occasional distinct cross walls without clamp connections.

The variability of the species will make it difficult to recognize at times. The essential characters seem to be the soft white plant widely effused on hardwoods, the tubes well developed, the hyphae with rather frequent cross walls (TEXT FIG. 1), and in addition one or more of the following characters: (a) well-developed hyaline projecting unincrusted cystidia; (b) capitate-incrusted paraphyses (?); (c) heavily incrusted irregular projecting cystidia; and (d) ellipsoid spores cohering in small groups.

PORIA INERMIS Ellis & Everhart, Proc. Acad. Nat. Sci. Philadelphia **1894**: 322. 1894

Original Description: Resupinate, adnate, seriate, extending along the limb for 6 in. or more and about 1 in. wide, yellowish-brown, 2–4 mm. thick in the middle, margin thin, narrow, light yellow (when fresh), and closely adnate; pores small, round, extending down to the underlying wood. Spores ferruginous, subglobose, 4–5 μ in diameter. (No spines).

On dead shrubs and limbs of various deciduous trees, Newfield, N. J. Received also from Michigan, Canada, Nebraska,

and Louisiana. Issued in N. Am. Fung. No. 313 as *P. obliquus* from which it is quite distinct.

Redescription: Perennial or at least persisting for three or four years, effused for 6–30 cm. in narrow elongated patches on small shrubs or branches and 1–3.5 cm. broad, inseparable, firm and corky in texture, with a narrow bright colored, yellow brown (honey yellow to clay color) sterile border rarely more than 1 mm. broad; subiculum extremely thin, inconspicuous, brown; tubes usually oblique, 1–3 mm. long, not stratified though increasing in length for several successive seasons, the mouths dark honey yellow to snuff brown or cinnamon brown, finally weathering to grayish brown, at first sub-rounded and minutely pubescent, then somewhat angular and more glabrous, averaging 3–4 per mm., the dissepiments rather thin but entire; hymenium much cracked in mature specimens; spores broadly ellipsoid and flattened on one side, or nearly globose, brown, smooth, 5–6 × 3–4 μ; cystidia and setae none; hyphae light to dark brown, mostly unbranched and with cross walls only in the lighter colored hyphae, no clamps, diameter 2.5–3 μ.

On dead limbs and trunks of a limited number of small shrubs; including *Alnus, Ilex*, and *Nemopanthus*.

Specimens Examined: Amherst, Massachusetts; Tripoli, West Fort Ann, and Bronx Park, New York; Scotia and Bear Meadows (three collections), Pennsylvania; Ann Arbor, Michigan.

Ellis and Everhart report the species, as will be noted, as occurring on limbs and shrubs of various deciduous trees, though no statement is made as to just what hosts are involved. The species is well represented at New York but I have not studied the collections, though Mr. Percy Wilson who has collected it many times tells me that he always finds it on *Ilex*. This and *Nemopanthus*, a closely related genus, represent the usual hosts on which I have been able to discover it, though Dr. P. J. Anderson sends me a Massachusetts specimen on *Alnus*, and I have myself made one collection on that host.

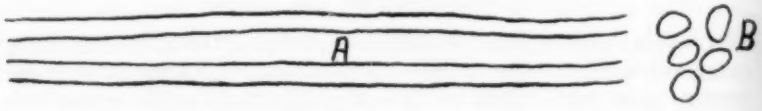


FIG. 2. PORIA INERMIS Ellis & Everhart. A, Hyphae from the trama; B, Spores.

The form assumed by the plant is characteristic (PLATE 14, FIGS, 5, 6), though necessitated by the smallness of the limbs or

trunks on which it grows. I have seen no specimens on trunks larger than 3.5 cm. in diameter and the average size is 2–2.5 cm. Since it nearly always grows on standing trunks the tubes are usually very oblique. In age the hymenium becomes cracked (PLATE 14, FIGS. 5, 6), due probably to the shrinkage caused by the drying out of the dead stem and by the decay brought on by the fungus. The margin of the plant is frequently quite irregular in outline or in older plants is apt to become somewhat thickened by reason of the receding growth of the fungus. The first year's growth is often not more than a millimeter thick. In old dead and dying specimens the margins of the fungus loosen somewhat from the substratum.

The species is one of the easiest of the Porias to identify. It is about the only brown species with brown spores, and brown spores in all specimens are nearly always to be found in abundance in the hymenium. The lack of setae is also noteworthy in brown Porias (PLATE 14, FIG. 7).

The original description reports the species from Canada, Michigan, Nebraska, and Louisiana. In this entire range various species of *Ilex* are present.

PORIA MEDULLA-PANIS (Pers.) Cooke, Grevillea **14**: 109. 1886

Boletus medulla-panis Pers. Syn. Method. Fung. 544. 1801.

Original Description: (Albus durus) effusus planus crustaceus, superne perforatus; tubulis obliquis (rectisque).

B. longissima, subterranea. Praesertim frequens ad ligna fabrefacta ex. gr. ianus vetustas, hortorum, aut in sylvis ad truncos aridos, inuenitus, oblique glaber, siccus. Pori pro loco et situ nuc recti, nunc oblique sunt.

Redescription: Annual or reviving for several years and eventually as much as 1 cm. thick, broadly effused for many centimeters, inseparable or separating only with difficulty, typically with a rather conspicuous pubescent or compactly tomentose margin, white to cream buff in color; subiculum a thin pallid layer that in old specimens practically disappears as such; tubes finally indistinctly stratified in three or four layers or sometimes distinctly so with thin layers of context separating the year's growth, 0.5–3 mm. long each season, the mouths pure white to antimony yellow or egg yellow, at first circular and thick-walled, often angular and thin-walled at maturity, always entire, often oblique, averaging 3–5 per mm.; spores ellipsoid

to oblong-ellipsoid or broadly ellipsoid, smooth, thin-walled, hyaline, 4–6 × 3–4 μ; basidia broadly clavate to pyriform, 5–8 μ in diameter; cystidia none or represented by pointed fusoid hyaline paraphysis-like bodies; abundant large crystals present in the tramal tissue and along the hymenium; hyphae very variable, in thin and compact collections from dry substrata rigid, much branched, 1.5–3 μ diameter; in better developed collections less branched or unbranched, 2–5 μ diameter; all without apparent cross walls and clamps.

On bark and wood of deciduous trees; recorded from *Acer*, *Artemisia*, *Castanea*, *Fagus*, *Fraxinus*, *Gleditsia*, *Liriodendron*, *Ostrya*, *Populus*, *Prunus*, *Quercus*, *Rhus*, *Robinia*, *Tilia*, and *Ulmus*. Often on fence posts and other structural timbers.

Specimens Examined: Ormstown, Quebec, Canada; North Conway, New Hampshire; Greenwood, Massachusetts; Knowersville, North Greenbush, and Sylvan Beach, New York; Westport, State College, and Greenwood Furnace, Pennsylvania; Richwood and Monmouth Junction, New Jersey; Chain Bridge, Maryland; Morgantown, Thomas, and Seneca, West Virginia; Arlington, Virginia; Fort Valley, Georgia; West Elkton (three collections), Oxford (eleven collections), and Cincinnati, Ohio; West Lafayette, Indiana; Geneseo and Cerro Gordo, Illinois; New Richmond, Frankfort, and Ann Arbor, Michigan; St. Louis County, Wicks, Meramec Highlands, and St. Louis, Missouri; Camp Pike, Arkansas; St. Paul, Minnesota; Blue Mounds, Wisconsin; Darby, Montana; Tolland, Colorado (three collections); Guadaloupe, California.

There are in my herbarium nearly sixty collections of this species with a range from New Hampshire to Georgia and west to California. As would be expected the species shows quite a bit of variation in this range. Bresadola and Murrill have already indicated *P. pulchella* Schw. as a synonym and after a close study of all these collections I find myself in agreement with them. I would also add *P. Xantholoma* Schw. to the list of synonyms. The species varies from a thin compact, rather hard plant (PLATE 14, FIG. 2), that often cracks on drying, to a more coriaceous or leathery plant (PLATE 14, FIG. 1) somewhat separable from the substratum. The first form is typical of the plant as it grows in dry exposed situations such as on fence posts, fence rails and structural timbers. This form usually has narrow rigid hyphae (TEXT FIG. 3) that are much branched and

less than 3 μ in diameter. The second form is more characteristic of the plant as it grows in more protected situations, and here the narrow rigid hyphae give place, entirely or in part, to wider and nearly simple hyphae 3–5 μ in diameter (TEXT FIG. 3). But all sorts of intergrading conditions exist so that neither on these characters nor on any others can the two forms be kept distinct. Then in coloration there is a nearly white form characteristic of plants where protected from the light, a gray or pallid form where exposed to considerable illumination, and finally a bright colored form with almost egg yellow hymenium whose relation to light I have not determined. This last form is more rarely met. I have specimens of it from New Jersey, Georgia, and Illinois. Through all these variations the hymenial characters are very constant (PLATE 14, FIGS. 3, 4). Spores are usually found in abundance (TEXT FIG. 3), even in crushed preparations of the hymenium, and often have a collapsed and empty appearance.

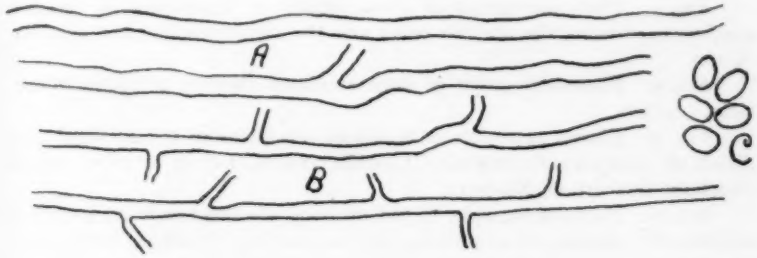


FIG. 3. PORIA MEDULLA-PANIS (Pers.) Cooke. A, B, Hyphae showing variations in amount of branching and considerable variation in diameter, the narrow, much branched ones being characteristic of the xerophytic form of the species; C, Spores.

The species is closely related to *P. subacida* Peck, which shows the same microscopic characters as the form of *P. medulla-panis* with the larger hyphae. Other microscopic characters possessed by both are the large basidia, the ellipsoid spores, and the abundance of crystals in the tramal tissue. Yet I have admitted here no specimens from a coniferous substratum, though perhaps the thick form referred to in a previous paper by me (Bull. N. Y. State Mus. 205–06: 114. 1919) should really be included here.

I am at present inclined to that opinion, but to admit these plants would extend the host range of this species to include wood of at least the main coniferous trees and give a gradation into typical *P. subacida* that would be extremely confusing. Yet in view of the close similarity in microscopic characters it might simplify matters to refer all these plants to such a one protean species.

STATE COLLEGE, PENNSYLVANIA

Explanation of plates 13 and 13

The photomicrographs in this paper are from free hand sections cut by the writer from herbarium specimens and mounted in glycerine. I have had the assistance of Mr. P. F. Shope in the preparation of the illustrations.

PLATE 13

PORIA CORTICOLA (Fr.) Cooke

FIG. 1. Photograph, × 1½. Overholts Herbarium, No. 5027.

FIG. 2. Same, showing older specimens but with a membranous margin and the tubes more or less collapsed. Overholts Herbarium, No. 4211.

FIG. 3. Photomicrograph of cross section of hymenium of Swedish specimens, showing the angular pores and the distribution of the cystidia, × 160.

FIG. 4. Photomicrograph of same specimen showing a cluster of cystidia, × 320.

FIG. 5. Closest approach in American specimens to the cystidial condition of European *P. corticola*. Cystidia represented at a, b, c, and d. Overholts Herbarium. No. 5912.

FIG. 6. Photomicrograph, × 320, showing the small capitate incrusted cystidia that project only slightly beyond the basidia. Overholts Herbarium, No. 8019.

FIG. 7. Photomicrograph, × 320, showing a somewhat more heavily incrusted cystidium sometimes present. Overholts Herbarium, No. 4211.

PLATE 14

FIGS. 1–4. PORIA MEDULLA-PANIS (Pers.) Cooke

FIG. 1. Photograph, × 1½, of a specimen of the more flabby and coriaceous type of this species. Overholts Herbarium, No. 5682.

FIG. 2. Photograph, × 1½, showing the harder, more adnate and general xerophytic type of the species. Overholts Herbarium, No. 4108.

FIG. 3. Photomicrograph, × 160, of cross section of the hymenium. Overholts Herbarium. No. 34.

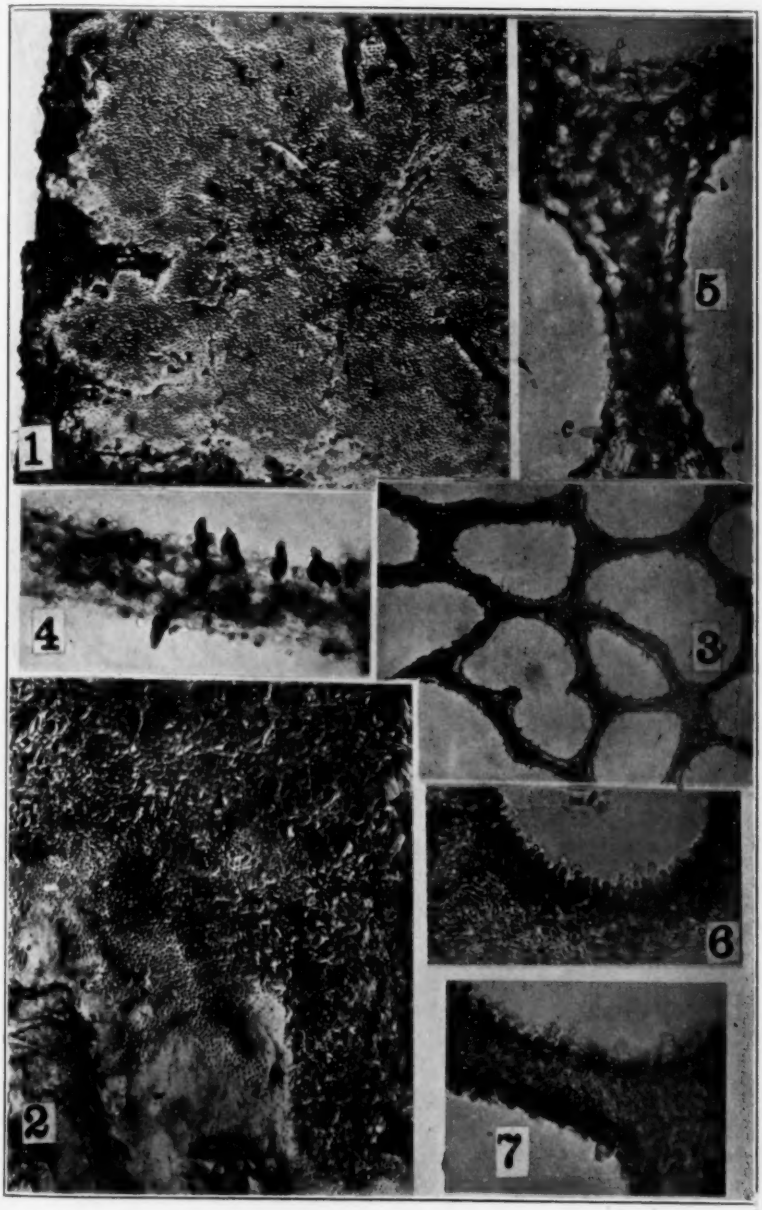
FIG. 4. Photomicrograph, × 320, showing small portion of the hymenial region of the same plant.

FIGS. 5–7. PORIA INERMIS Ellis & Everhart

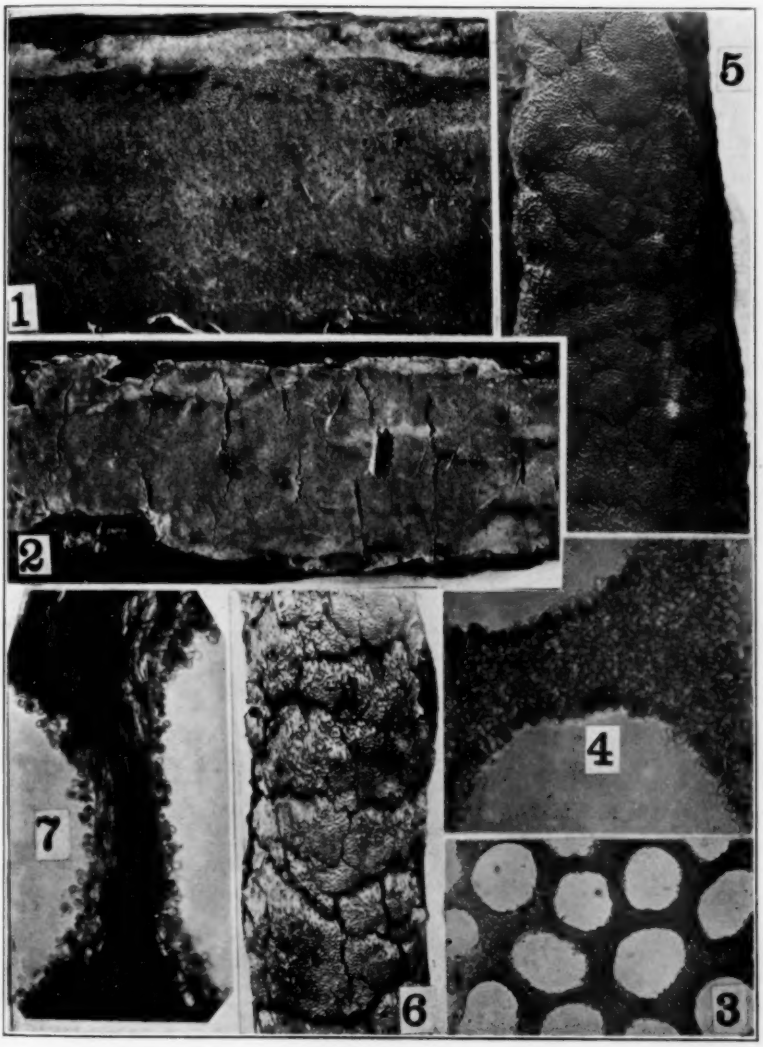
FIG. 5. Photograph, × 1½, of the usual type of the species, with a narrow sterile margin and the hymenium showing somewhat of a tendency to crack. Overholts Herbarium No. 5432.

FIG. 6. Photograph, × 1½, of an older specimen, somewhat discolored and with the hymenium much cracked. Overholts Herbarium No. 4794.

FIG. 7. Photomicrograph, × 320, showing portion of the hymenium, with absence of setae and with the brown globose spores. Overholts Herbarium, No. 4794.



PORIA CORTICOLA (FR.) COOKE



1–4. PORIA MEDULLA-PANIS (PERS.) COOKE
5–7. PORIA INERMIS ELLIS & EVERHART

INDEX TO AMERICAN BOTANICAL LITERATURE
1920-1922

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to foresty, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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